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Ecological significance of blue light stimulation of photosynthetic capacity in *Laminaria* spp. and other brown algae

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ABSTRACT: The transient stimulation of light-saturated photosynthesis in *Laminaria digitata* (Huds.) Lamour. and *L. saccharina* (L.) Lamour., which has been observed following pulses of blue light, was found to persist when low irradiances of continuous blue light were given as a supplement to saturating irradiances of red or yellow light. The degree of stimulation was directly proportional to the logarithm of the irradiance of blue light, with a 50% response at 0.28 µmol m^{-2} s^{-1} and saturation above 1 µmol m^{-2} s^{-1}. These irradiances represented about 0.2% and 0.5%, respectively, of the total irradiance incident on the plants. In natural underwater light fields, such low proportions of blue wavelengths would be found only close to, or below, the lower depth limit for *Laminaria* spp., where photosynthesis, if it occurred at all, would be light-limited and, therefore, not subject to blue light stimulation. Irradiances of blue light measured in the *Laminaria* zone during periods when the total irradiance was high enough to saturate photosynthesis were always higher than 1 µmol m^{-2} s^{-1}, and photosynthesis by *Laminaria* spp. in simulated underwater light fields in the laboratory was not affected by additional blue light. Unlike *Laminaria*, other brown algae (e.g. *Asperococcus*, *Ectocarpus*) exhibited stimulation by blue light in irradiances of red light which are limiting for photosynthesis, and their photosynthetic rates can, therefore, be limited when blue light is present as a higher proportion of the total irradiance than for *Laminaria*. However, these plants are mostly found in the littoral zone, and will rarely experience low blue light environments. The stimulation of photosynthetic capacity by blue light in brown algae occurs at such low irradiances of blue light that photosynthesis by these plants, in their natural habitats, is unlikely ever to be limited by a shortage of blue light.

KEY WORDS: Blue light · Brown algae · *Laminaria* · Light quality · Photosynthesis · Underwater light

INTRODUCTION

The rates of photosynthesis by most species of brown algae in saturating irradiances of red light increase rapidly after brief exposure of the plants to low irradiances of blue light, and this stimulation continues for 1 to 2 h following the blue light pulse (Dring 1989, Forster & Dring 1994). The physiological reasons for this stimulation of photosynthetic capacity by blue light cannot be related to the Emerson enhancement effect because, in most species, it is not observed in limiting irradiances of red light, and because the broad-band red light fields that have been used contain wavelengths that are absorbed by both photosystems in brown algae. Rather than influencing the 'light reactions' of photosynthesis, blue light appears to stimulate the rate of supply of inorganic carbon to the plant from the external seawater, since the degree of response to a standard pulse of blue light decreases as the dissolved inorganic carbon (DIC) concentration of the seawater is increased (Forster & Dring 1992). Several details of the photobiology of the photosynthetic responses of brown algae to pulses of blue light (e.g. dose-response curve, action spectrum, kinetics)

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have now been established and compared with other responses of plants to blue light (Schmid & Dring 1992, 1993a, b, Schmid et al. 1994). One aspect of these responses which has not so far been examined in detail, however, is the role that blue light may play in controlling photosynthesis by brown algae in their natural habitat. For this reason, the influence of long-term treatments with blue light has been studied and related to the spectral composition of the light to which brown algae are exposed in typical underwater sites.

METHODS

Plant material. First-year sporophytes of *Laminaria digitata* (Huds.) Lamour. and of *L. saccharina* (L.) Lamour. with blades up to 15 cm long, and plants of *Asperococcus* sp., were collected from the lower intertidal zone at Ballyhenry Island, Co. Down, Ireland (Irish Grid ref.: J574521). Plants were brought back to Belfast in seawater within 2 h of collection, trimmed to a blade length of 5 cm, and stored in 2 l flasks of aerated seawater at 15°C and 50 µmol m^{-2} s^{-1} with 16 h light d^{-1} from 04:00 to 20:00 h. All plants were used for experiments within 2 wk of collection.

Photosynthesis measurements. Photosynthetic rates were estimated from oxygen-electrode readings using either a closed-cell or a flow-through system. For the closed-cell system, sections of *Laminaria* spp. blade (3 × 1.5 cm, fresh wt 0.05 to 0.1 g) were suspended in a cylindrical glass chamber, and the oxygen concentration in the chamber was monitored continuously by an electrode connected to a computer (for details, see Forster & Dring 1992). Gross photosynthesis was estimated by adding the mean rate of oxygen uptake in dark periods preceding and following the photosynthesis measurements to the rate of net oyxgen evolution in each light treatment. Better time resolution was obtained with the flow-through system, in which small pieces of plant material were fixed directly to the surface of the electrode with dialysis membrane, and placed in continuously flowing seawater (for details, see Schmid & Dring 1992). Both systems were deployed in a water bath at a temperature of 15.0 ± 0.1°C.

Light treatments. Broad-band red and blue light fields were obtained by filtering the light from quartz-halogen projector lamps through Plexiglas filters (Röhm, Darmstadt, Germany; No. 603, 425 to 515 nm with peak at 470 nm; No. 501, 580 to 720 nm with peak at 630 nm) although for some experiments with the flow-through system, red light was provided by an array of light-emitting diodes (peak emission 661 nm, half-bandwidth ca 30 nm; see Schmid & Dring 1993b). For yellow light fields, a Plexiglas cut-off filter with 50% transmittance at 540 nm and 2% transmittance at 500 nm was combined with a quartz-halogen lamp. The simulated underwater light field 'I5' (Schott filters 2 mm BG18 + 1 mm GG4 combined with quartz-halogen light; Lüning 1980) had a similar spectral composition to light at 2 to 6 m depth in coastal water type 5 (Jerlov 1976). Irradiance at the plant surface in all light fields was measured with cosine quantum sensor (Li-Cor, Lincoln, NB, USA). Control of the irradiance of blue light was achieved with neutral density filters (Oriel, Stamford, CT, USA)

RESULTS AND DISCUSSION

In order to increase their ecological relevance, preliminary experiments on the effects of continuous blue light on the photosynthetic rate in *Laminaria digitata* were conducted against a background of yellow light (or, more strictly, all visible wavelengths except blue) rather than against red wavelengths alone. The irradiance of yellow light required to saturate photosynthesis in this species was determined by increasing the irradiance in steps until no further increase in photosynthesis was observed. This maximal rate of photosynthesis in yellow light was stimulated by 1 min pulses of blue light, but the rate decayed back to the unstimulated rate within 30 to 40 min (Fig. 1). Thus, plants photosynthesising in yellow light responded to blue light pulses in the same way as plants in red light (compare with flow-through traces for *L. saccharina* in

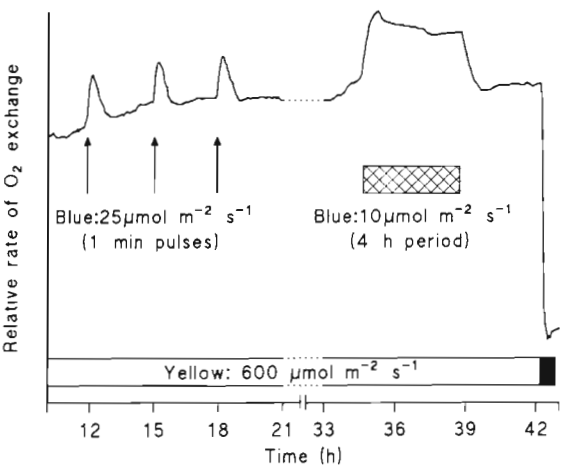

Fig. 1 *Laminaria digitata*. Changes in rates of oxygen exchange with time using a flow-through system for a small section of blade exposed to a saturating irradiance of yellow light, and 1 min pulses or a 4 h period of supplementary blue light at the irradiances indicated. Final section of trace indicates rate of oxygen exchange in darkness (solid portion of horizontal bar). Zero on *x*-axis represents midnight on the day the experiment started

Schmid & Dring 1993b, Schmid et al. 1994). Addition of continuous blue light to saturating yellow light resulted in a similarly rapid increase in photosynthesis, but the photosynthetic rate decayed only slightly over the next 30 min and remained above the rate in red light for over 4 h (Fig. 1). When the blue light was switched off, the rate of decay of photosynthesis was similar to that after the 1 min pulses, and decay was complete within 40 min. In other experiments with *L. digitata* (not shown), an increased rate of photosynthesis was maintained in the presence of blue + yellow light for up to 16 h, but always decreased rapidly when the blue light was switched off.

The degree of stimulation by continuous blue light over the rate of photosynthesis in saturating yellow light was dependent on the irradiance of the supplementary blue light, and increased substantially between 3 and 10 µmol m^{-2} s^{-1} (Fig. 2). Switching from yellow + blue light (600 + 10 µmol m^{-2} s^{-1}) to white light at 600 µmol m^{-2} s^{-1} resulted in a further increase in photosynthetic rate, but this decreased slowly over the next 6 h before reaching a rate which remained constant for the rest of the experiment (a further 12 h; Fig. 2). The final rate of photosynthesis in white light was similar to that in yellow light supplemented with

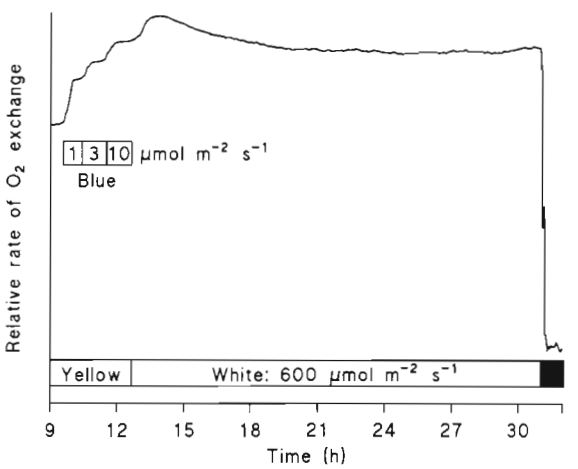

Fig. 2. *Laminaria digitata*. Changes in oxygen exchange rates with time using a flow-through system for a small section of blade exposed to a saturating irradiance of yellow light (600 µmol m^{-2} s^{-1}) alone and with supplementary blue light at the irradiances and for the periods indicated by the bar labelled 'Blue', followed by a saturating irradiance of white light. Initial rate was that in saturating yellow light, and final section of trace indicates rate of oxygen exchange in darkness. 'White' was the unfiltered light from a quartz-halogen projector lamp, 'Yellow' was the same light with all blue wavelengths removed by a Plexiglas filter, and 'Blue' was the standard broad-band blue field used in this investigation. Zero on *x*-axis represents midnight on the day the experiment started

3 to 10 µmol m^{-2} s^{-1} of blue light. This result indicates that the photosynthetic rate of *Laminaria* spp. in a saturating irradiance of white light (even a 'white' light with as small a proportion of blue wavelengths as the unfiltered light from a quartz-halogen bulb; only 5.9% of PAR is at wavelengths < 500 nm, according to spectrum measured by Lüning & Dring 1985) is equivalent to the photosynthetic rate in red or yellow light plus the full stimulation achievable by a low irradiance of continuous supplementary blue light. It is not clear why the photosynthetic rate should have increased immediately after transfer from yellow + blue light into white light (Fig. 2) but, when using the flow-through system, almost every change in light regime resulted in an immediate and strong photosynthetic response, followed by a relaxation of the response to a steady rate over the next 1 to 3 h (e.g. yellow to yellow + blue, Fig. 1; red 275 to red 18, Fig. 6; red 30 to red 130, Fig. 7; and measurements with *Ectocarpus* in Schmid et al. 1992). This was observed even when changing from one light-saturating irradiance to another, higher irradiance (results not shown). Photosynthetic rates in brown algae, therefore, typically exhibit a period of acclimation following most changes in light regime (see further discussion below).

The dependence of the photosynthetic response on the irradiance of supplementary blue light was examined in detail by exposing plants for 2 h to different irradiances of blue light against a background of saturating red light (200 µmol m^{-2} s^{-1}; Fig. 3). In order to allow for variations in the absolute photosynthetic rates and in the responses to blue light of different plants, the stimulation measured in each irradiance of blue light was expressed as a percentage of the stimulation caused by a standard high irradiance of blue light (50 µmol m^{-2} s^{-1}) in each plant. Significant stimulation was caused by the lowest irradiance tested (0.01 µmol m^{-2} s^{-1}), but the degree of stimulation increased in a hyperbolic manner, with saturation being approached at irradiances above 1 µmol m^{-2} s^{-1} (Fig. 3a). When stimulation was plotted against the logarithm of irradiance (Fig. 3b), a linear irradiance-response curve was obtained with little sign of saturation up to the reference maximum of 50 µmol m^{-2} s^{-1}. On a linear scale, however, the slope at irradiances above 1 µmol m^{-2} s^{-1} was so low that it barely exceeded the variability of the measurements. The regression fitted to the data predicted that 50% stimulation would be achieved at an irradiance of 0.28 µmol m^{-2} s^{-1}. An earlier investigation with the same species (Dring 1989) had shown that the pulses of blue light which produced either saturation or a 50% response contained quantum exposures of 5 and 1.5 mmol photons m^{-2}, respectively (the latter value has been calculated from the cited regression). Since both of

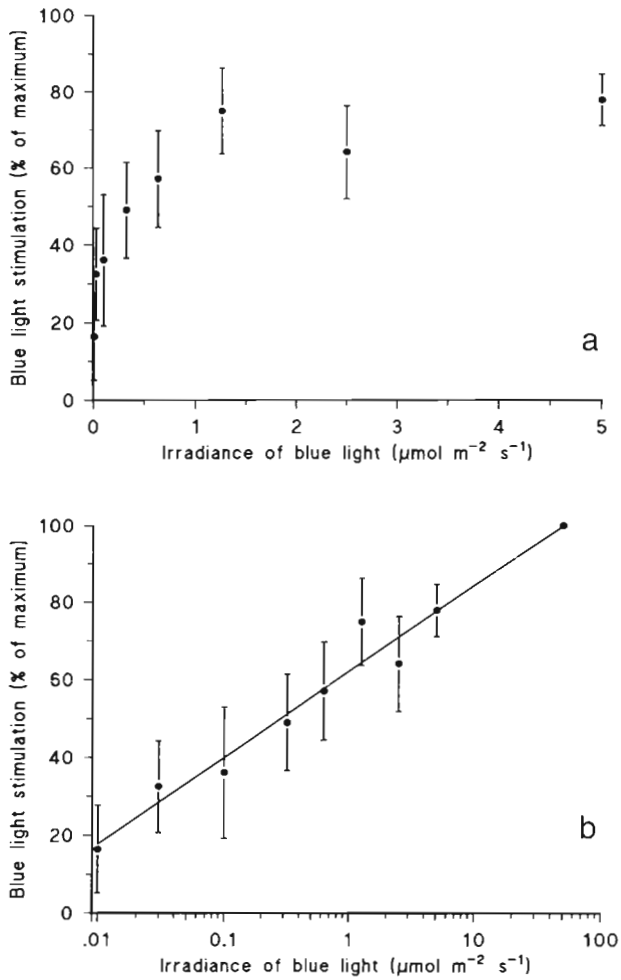

Fig. 3. *Laminaria digitata*. Effect on net photosynthesis of different irradiances of blue light given continuously over 2 h periods as a supplement to a saturating irradiance of red light (200 μmol m^{-2} s^{-1}). (a) Irradiance scale linear; (b) irradiance scale logarithmic. Photosynthesis was measured in the closed-cell system after a steady rate had been reached in each irradiance of blue light (usually after about 1 h). The differences between these rates and the unstimulated rate of photosynthesis of the same plant in red light are expressed as a percentage of the stimulation measured for the same plant in 50 μmol m^{-2} s^{-1} of blue light at the end of the series of irradiances. At least 5 separate plants were measured at each irradiance, and the error bars indicate 95% confidence limits. Regression line in lower figure has the equation: $y = 62.522 + 22.611 \log(x)$; $r^2 = 0.963$, where y is the degree of blue light stimulation (%) and x is the blue light irradiance (μmol m^{-2} s^{-1})

these values are equivalent to about 90 min treatment with the irradiances determined in this study, the sensitivity of the system to blue light given continuously seems to be similar to that given as short pulses.

The estimates of the irradiances of continuous blue light required to produce 50% of its influence on photosynthetic rate, or to saturate the response, can also be expressed as the percentage of the total irradiance to which the plant was exposed. Thus, 50% stimulation was achieved by less than 0.2% of the total irradiance (i.e. 0.28 μmol m^{-2} s^{-1} expressed as a percentage of 200 μmol m^{-2} s^{-1}), whereas the response to blue light was saturated by about 0.5% of the total irradiance. These values can then be compared with measurements of the proportion of blue light in natural underwater habitats. The spectral composition of light at various depths in coastal water types (Coastal) 5, 7 and 9 was calculated from Jerlov's (1976) values for spectral transmittance of different water types, and the ratio of blue (400 to 475 nm) to green + red (500 to 700 nm) light ['B/(G+R)'] was plotted against depth (Fig. 4). The ratio decreased exponentially with depth in all water types, but the rate of decrease was greatest in Coastal 9. The critical value of this ratio for *Laminaria* spp. (0.5%), below which photosynthesis might be limited because blue light stimulation was not fully expressed, was reached at about 6 m in Coastal 9, 16 m in Coastal 7 and 35 m in Coastal 5. A depth of 6 m in Coastal 9 coincides with the '1% depth' (i.e. the depth at which the total irradiance is 1% of its surface value), which is also the depth at which the deepest plants of *Laminaria* spp. are normally found. However, the growth of *Laminaria* spp. towards the bottom of their zone is known to be light-limited (e.g. Kain 1966), so that their photosynthesis at this depth is unlikely to be light-saturated. Therefore, blue light will probably have little influence on the photosynthetic rates of *Laminaria* spp. at this depth. The depths at which the B/(G+R) ratio reaches 0.5% in the clearer water types

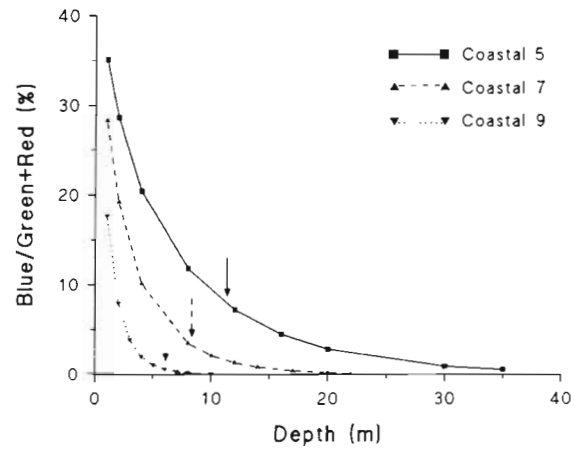

Fig. 4. Effects of water depth and Jerlov water type on the ratio of irradiance in blue (400 to 475 nm) to that in green + red (500 to 700 nm) wavebands. Values calculated from spectral transmittance data of Jerlov (1976). Arrows indicate depths in each coastal water type (Coastal) at which total irradiance is 1% of surface value

(16 m in Coastal 7; 35 m in Coastal 5) are well below the 1 % depths in these waters (8 m and 11.5 m, respectively). These results, therefore, suggest that photosynthesis by *Laminaria* spp. growing in natural conditions will never be limited because there is insufficient blue light to saturate the photosynthetic response of these plants to blue light.

This conclusion was supported by 2 other approaches to the problem. Firstly, continuous records of underwater irradiance in 3 wavebands during August and September 1990 (measured as described by Dring & Lüning 1994) demonstrate that, whenever the total irradiance in green + red at a depth of 4.5 m was high enough to saturate photosynthesis (i.e. >50 µmol m^{-2} s^{-1}), the irradiance in blue was always greater than 1.5 µmol m^{-2} s^{-1} and was usually > 3 µmol m^{-2} s^{-1} (Table 1). These irradiances of blue light are sufficient to cause complete stimulation of photosynthetic capacity. Secondly, the photosynthetic rate in *Laminaria* spp. in a saturating irradiance of 'white' light, whose spectral composition was similar to that in 2 to 6 m depth in Coastal 5 ('I5'), was not affected by a 2 min pulse of blue light (Fig. 5). These data suggest that there is sufficient blue light in light fields typical of the natural habitat of *Laminaria* to saturate the demand for blue light by the photosynthetic apparatus.

This negative assessment of the role of blue light in determining the photosynthetic rate of *Laminaria* in the sea should not be extrapolated to all brown algae without further examination. A recent survey of the photosynthesis of 18 species of brown algae in red light before and after pulses of blue light (Schmid et al. 1994) has shown that the responses of *Laminaria* are typical of one group of species (members of the Laminariales, Fucales and Dictyotales) but differ markedly from those of another group of species (members of the Ectocarpales, Chordariales and Dictyosiphonales). The most obvious difference between the 2 groups was that species in the latter group exhibited a circadian rhythm of photosynthesis in a continuous saturating irradiance of red light (e.g. peaks of photosynthesis at 36 and 60 h in *Asperococcus* sp., Fig. 6), which was rarely, if ever, apparent in *Laminaria* spp. The maximum size of the photosynthetic response to a pulse of blue light, and several aspects of the kinetics of the response, also differed between the 2 groups. For example, the maximum rate of photosynthesis following a blue light pulse in *Asperococcus* sp. was up to 300 % higher than in a saturating irradiance of red light (Red 275, in the troughs of the photosynthetic rhythm; Fig. 6), compared with 50 % or less in *Laminaria* spp., and the stimulation persisted for 1.5 to 2 h instead of for 30 to 40 min in *Laminaria* spp.

In the present context, however, the most important difference between the blue light responses of some

Table 1 Typical values of irradiance (expressed as hourly means; µmol m^{-2} s^{-1} 100 nm^{-1}) in 3 wavebands at 4.5 m depth off Helgoland, Germany (North Sea), and the ratio of irradiance in blue light to the sum of irradiances in green and red light [B/(G+R)], during 1 h periods in August and September 1990 when total irradiance was just high enough to saturate photosynthesis in *Laminaria* spp. (i.e. about 50 µmol m^{-2} s^{-1}). The water type, as estimated each day from the mean transmittance of the green waveband, was Coastal 7 on 31 August and 26 September, and Coastal 5 on all other days. For details of light measuring station, see Dring & Lüning (1994)

Date	Time (h)	Hourly means of irradiance Blue	Green	Red	B/(G+R) (%)
14 Aug	9–10	7.29	53.90	9.60	11.47
	15–16	6.56	48.21	6.17	12.06
15 Aug	9–10	5.68	46.63	6.98	10.59
	12–13	14.53	49.23	11.95	23.76
16 Aug	9–10	5.78	42.11	5.63	12.10
	16–17	7.01	42.68	6.31	14.31
29 Aug	9–10	3.23	39.55	7.08	6.92
	12–13	3.22	43.13	6.88	6.43
31 Aug	12–13	1.53	40.73	5.38	3.31
	13–14	4.95	38.49	8.25	10.59
12 Sep	9–10	8.51	38.15	8.73	18.15
	12–13	7.43	38.33	7.34	16.28
13 Sep	10–11	8.44	41.03	8.97	16.88
	14–15	9.36	40.07	8.31	19.35
14 Sep	12–13	13.79	46.60	11.39	23.77
	15–16	11.65	50.05	9.44	19.59
16 Sep	12–13	8.93	54.38	9.17	14.05
	16–17	13.23	46.67	11.99	22.55
26 Sep	10–11	6.22	36.54	9.05	13.63
	11–12	6.43	36.20	8.96	14.23

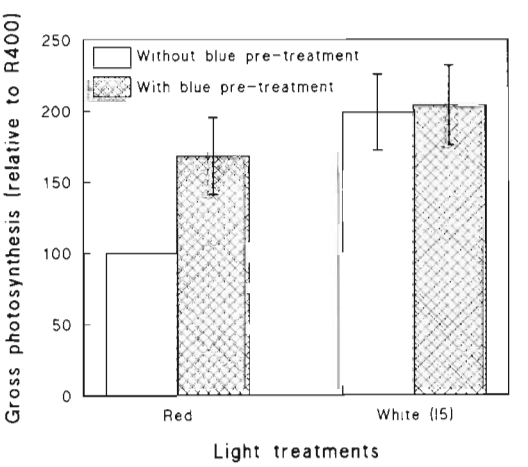

Fig. 5. *Laminaria digitata*. Effect of pre-treatment with blue light (50 µmol m^{-2} s^{-1} for 2 min) on gross photosynthetic rate in saturating irradiances (400 µmol m^{-2} s^{-1}) of either red or white ('I5') light. The 'white' light source was a quartz-halogen projector lamp filtered through Schott glass filters (2 mm BG38 + 1 mm GG4) to give a spectral distribution similar to that in 2 to 6 m depth in coastal water type 5 (Lüning 1980). The rates of photosynthesis of 5 separate plants in all light treatments were measured in the closed-cell system and expressed relative to the rate of each plant in saturating red light without blue pre-treatment (i.e. 'R400' = 100). Error bars indicate 95 % confidence limits on the means for all other treatments

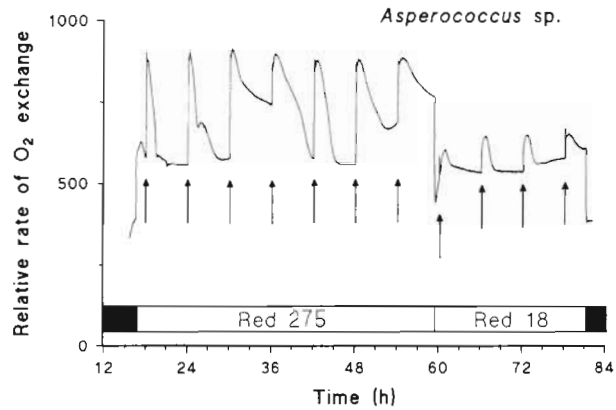

Fig. 6. *Asperococcus* sp. Time-course of changes in photosynthetic oxygen evolution, measured in a flow-through oxygen-electrode system at 15°C, in 2 irradiances of red light and after pulses of blue light. Horizontal bar indicates darkness and red light treatments: 275 and 18 (irradiances in µmol m^{-2} s^{-1}); arrows indicate pulses of blue light (each 1 min at 7 µmol m^{-2} s^{-1}). Zero on *x*-axis represents midnight on the day the experiment started

rhythmic species and those in *Laminaria* spp. was that stimulation was not confined to irradiances of red light which saturated photosynthesis. In *Asperococcus* sp., blue light pulses still caused a 60% increase in photosynthesis when the irradiance of red light was reduced to 18 µmol m^{-2} s^{-1} (Red 18, Fig. 6) and the photosynthetic rate in red light alone was equivalent to that during the troughs of the rhythm at higher irradiances. Blue light stimulation was also observed in *Ectocarpus* in irradiances of red light which were limiting for photosynthesis (Schmid et al. 1992). In *Laminaria saccharina*, on the other hand, there was

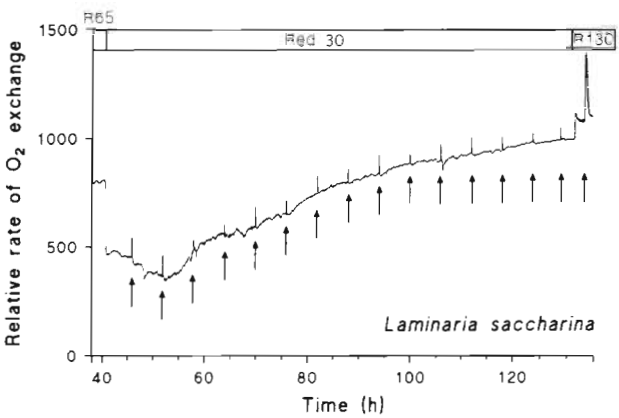

Fig. 7. *Laminaria saccharina*. Effects of a decrease in red irradiance on the rate of photosynthetic O_2 evolution and its response to pulses of blue light over several days. Other details as in Fig. 6

no stimulation of photosynthesis — beyond that attributable to the extra photons available during the pulse itself — even after 90 h in a low irradiance of red light (Red 30, Fig. 7), although a typical stimulation response was detected shortly after the plant's transfer back to saturating red light (R130, Fig. 7). These differences in response between *Laminaria* spp. and 2 species of brown algae with thin thalli may represent an additional characteristic which differentiates species with a strong circadian rhythm of photosynthesis in red light from those with a weak rhythm (see Schmid et al. 1994), although more species need to be tested under light-limited conditions before this conclusion can be confirmed.

Since the photosynthesis of some species of brown algae can be stimulated by blue light under irradiances which are limiting for photosynthesis, blue light could control photosynthetic rate when it represents a higher percentage of the total irradiance than was critical for *Laminaria* spp. Assuming that, as in *Laminaria* spp., continuous blue light at 1 µmol m^{-2} s^{-1} would be sufficient to saturate the photosynthetic response of *Asperococcus* sp., blue light would become limiting if it were less than about 5% of a total irradiance of 18 µmol m^{-2} s^{-1} (using the example in Fig. 6). A 'B/(G+R)' ratio of 5% would occur at a depth of < 3 m in Coastal 9, at about 7 m in Coastal 7 and at 15 m in Coastal 5 (Fig. 4). Although these depths are above the 1% depth in Coastal 7 and 9, they are greater than would normally be experienced by algae, such as *Asperococcus* or *Ectocarpus*, which inhabit the intertidal, rather than the sublittoral, zone of the shore. Since it is only in intertidal species of brown algae that blue light has so far been shown to stimulate light-limited photosynthesis, we must again conclude that the photosynthesis of brown algae in the field is unlikely to be limited directly by a shortage of blue quanta in the incident light.

Nevertheless, during our studies of this stimulation of photosynthesis by blue light, we have obtained preliminary evidence that both the rate and the extent of the acclimation of photosynthesis in brown algae following a change in irradiance (see examples listed earlier) or DIC supply (e.g. in *Ectocarpus*, Schmid et al. 1992) is affected by the presence of blue light. Therefore, the photosynthetic response to blue light may be a mechanism which contributes to the ability of brown macroalgae to optimise their photosynthetic rate to the prevailing environmental conditions. Further studies of the ecological significance of this response will concentrate on this possibility.

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